

SENSILLA ON THE ANTENNAE, FORETARSI AND PALPI OF
MICROPLITIS CROCEIPES (CRESSON)
(HYMENOPTERA: BRACONIDAE)

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Abstract.—Sensory receptors on the antennae, labial and maxillary palpi, and foretarsi of *Microplitis croceipes* (Cresson) were examined by scanning electron microscopy. The occurrence of antennal sensilla not described by earlier workers is reported. Generally, there are 6 types of sensilla in adults of *M. croceipes*, namely, sensilla (s.) trichodea, s. basiconica, s. chaetica, s. placodea, s. campaniformia and s. coeloconica. Sensilla placodea, campaniformia and coeloconica occur only on antennal flagella. However, s. trichodea and s. basiconica were present on all structural parts examined. Variants of s. trichodea (Trichodea A, B, C and D) and those of s. basiconica (Basiconica A and B) are described. The present paper documents for the first time the occurrence of Trichodea B, C and D, Basiconica B, s. chaetica, s. campaniformia and s. coeloconica in *M. croceipes*. Sexual dimorphism in *M. croceipes* correlates with antennal sensilla type; s. campaniformia are present only on female antennae whereas s. coeloconica and bent-tipped trichoid sensilla (D) occur only on male antennae. Other sensilla types occur in both sexes.

Key Words: Sensilla, antennae, foretarsi, labial palps, maxillary palps, sexual dimorphism

Insects are generally heavily vested with hairs (sensilla) used for olfactory, gustatory, hygro-, mechano-, and thermo-reception (Ramaswamy and Gupta 1981). The responses of various sensilla may vary with insect structural parts (O'Connel 1975), between insects (Dethier 1977), gender and age after ecdysis, or emergence (Zacharuk 1980). Detection of chemotactic stimuli by insects is mediated by sensory receptors present on the antennae, mouthparts, and tarsi (Frings and Frings 1949, Weseloh 1972). In *Blatella germanica* (L.) pheromone detection is mediated by sensory receptors on the antennae and on the maxillary and labial palps (Ramaswamy and

Gupta 1981). Sensory organs on the mouthparts and tarsi have been found to influence feeding in *Phormia*, *Tabanus*, *Locusta* and *Chrysomela* species, whereas those on the tarsi of *Pieris brassicae* (L.), *Delia brassicae* Bouche, *Psila rosae* (F.), *Rhagoletis* sp. and *Ceratitis* sp. are involved in oviposition (Stadler 1980). Antennal sensory receptors in parasitic wasps play an important role in host choice, including detection of ovipositional and host recognition cues (Weseloh 1972, Barlin and Vinson 1981). Insects may also rely on chemoreceptors found on the labial and maxillary palpi in addition to those found on the antennae in perceiving host plant chemicals, as in *Choristoneura*

fumiferana (Clemens) (Tortricidae) (Albert 1980). Given the apparent importance of antennal sensory receptors in parasitoids, morphological studies of these structures have been numerous. Norton and Vinson (1974b) compared the antennal sensilla of the braconids *Cardiochiles nigriceps* Viereck and *M. croceipes* and the ichneumonid *Campoletis sonorensis* (Cameron). In *M. croceipes* trichoid, basiconic, and placoid sensilla were described. In this paper we document the presence of previously undescribed sensory organs on the antennae, foretarsi, and labial and maxillary palpi of *M. croceipes*.

METHODS AND MATERIALS

Adults of *M. croceipes* were reared from *Heliothis virescens* (F.) larvae grown on artificial diet (King and Hartley 1985). Samples for scanning electron microscopy were either prepared in a Hexland Cryo Trans 1000 (HCT) apparatus which allows for examination of frozen hydrated biological specimens, or dehydrated serially in ethanol, critical point dried prior to coating with gold/palladium and mounted using silver paint. For HCT preparation, live wasps were held individually inside gelatin capsules (size 00), immobilized by cold treatment for 2–3 min, and mounted on conductive aluminum stubs using O.C.T. compound (Tissue Tek, Miles Laboratories, Inc., Naperville, Illinois) as an embedding medium. Mounted specimens were frozen in nitrogen slush for 10–15 s, sputter coated with gold for 2 min, and examined at -185 to -120 C in a JEOL JSM 840 scanning electron microscope at accelerating voltage of 5–15 kV.

The presence of pores in receptor organs indicates chemosensory function. The porosity of trichoid and basiconic sensilla on the antennae was determined by a silver staining technique modified after Schafer and Sanchez (1976). Live insects were washed 3 times in 10% acetone for 10 s each wash, placed on 0.1 M AgNO_3 for 3–6 min

and washed 3 times in distilled water for 15 min each wash. The insects were later soaked in Kodak Microdal-X developer for 5–7 min, rinsed in 3% acetic acid for 1 min and dehydrated serially in ethanol. Dehydrated specimens were cleared in xylol/phenol mixture (3:1 ratio + 1% ethanol) and mounted in Hoyer's medium. Mounted specimens were examined using a compound light microscope.

Description and classification of sensilla in the present study were based mainly on external form (outgrowth), reticulations (grooves), mode of insertion (sockets) and porosity (stainability). The thickness and number of pores (uniporous vs. multiporous) of the cuticular walls were not determined. Sensilla dimensions were measured in terms of length and basal width (at widest point) of projection (trichoid and basiconic sensilla), diameter of basal plate and papilla (campaniform sensilla), diameter of cellular ring and length and basal width of peg (coeloconic sensilla).

RESULTS

In general six types of sensilla (Table 1) were observed on the antennae, foretarsi and palpi of *M. croceipes* adults: sensilla (s.) trichodea, s. basiconica, s. chaetica, s. placodea, s. campaniformia and s. coeloconica. No attempt was made to classify and describe variants of trichoid and basiconic sensilla on the bases of their internal structures. All sharply pointed hairlike or setaceous projections were treated as s. trichodea; variations in size, reticulations and structural curvature were grouped as subtypes (variants). Four variants of s. trichodea (Trichodea A, B, C and D) and two subtypes of s. basiconica (Basiconica A and B) are described in the present study.

SENSILLA TYPES

Sensilla Trichodea A (Figs. 1, 3, 5, 9, 11, 13, 16): These long, slender hairs taper gradually to a point and project from nonsocketted insertions. They bear longitudinal or

Table 1. General types of sensilla on *Microplitis croceipes* (Cresson).

Sensilla	Type/ Variant	Structural Part Examined			
		Antenna	Foretarsus	Max. Palpus	Lab. Palpus
Trichodea	A	+	+	+	+
	B	-	+	-	-
	C	+	-	-	-
	D	-	+	-	-
Basiconica	A	+	+	+	+
	B	+	-	-	-
Chaetica		+	-	-	-
Placodea		+	-	-	-
Campaniformia		+	-	-	-
Coeloconica		+	-	-	-

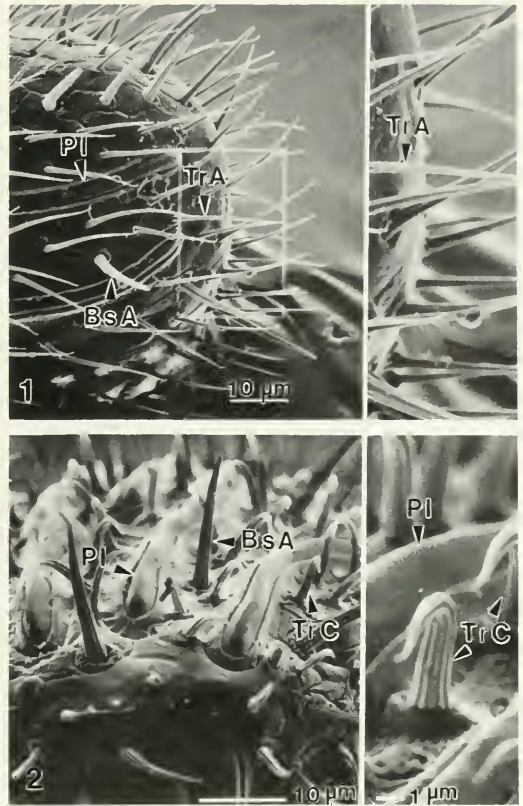
+, Present; -, Absent.

spiral grooves sculptured prominently along the length of the shaft. Trichodea A found on the antennae are ca. 35.6 μm long and 2.4 μm wide. Those on the foretarsus are ca. 44.5 μm long and 3.0 μm wide.

Sensilla Trichodea B (Figs. 11, 12): These hairlike sensilla are as long as Trichodea A and they similarly terminate to a sharp point. However, the shafts are twice (6.1 μm) as wide at the base and they taper abruptly near the tips, creating a robust and bulky appearance. These hairs are found mostly on the foretarsus.

Sensilla Trichodea C (Fig. 2): Although similar to what had been described by Norton and Vinson (1974b) in *C. nigriceps* as bent-tipped basiconic sensilla, these hairs conform more with trichoid characteristics and are, therefore, classified as one type of s. trichodea. Their occurrence on the antennae of *M. croceipes* was not reported in earlier literature. These sensilla occur abundantly on the ultimate flagellomere of male antennae. The hair bends at about $\frac{2}{3}$ of the shaft length and tapers to an upward curl forming an s-shape. The shaft is markedly grooved and projects from a slightly raised socket.

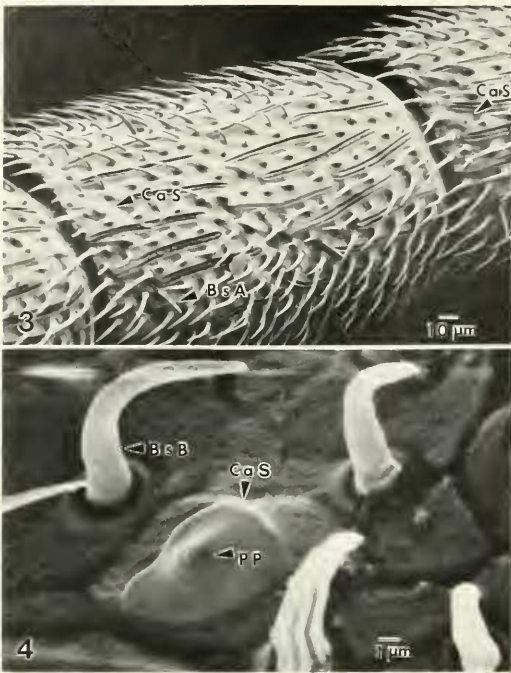
Sensilla Trichodea D (Figs. 9, 15, 16): These sensilla are long and slender (2.7 \times 2.5 μm) and similar to Trichodea A. Each



Figs. 1, 2. Flagellomere 16 of female (1) and male (2) antennae. Basiconic sensilla A (BsA); placoid sensilla (Pl); trichoid sensilla A (TrA); trichoid sensilla C (TrC).

hair, however, projects from a nonsocketed insertion and terminates to a fine hook. The length of the shaft is longitudinally or spirally grooved.

Sensilla Basiconica A (Figs. 1-3, 9, 10, 15, 17): Basiconic sensilla are blunt-tipped sensory hairs which may vary in size, surface sculptures and plane of projection relative to the cuticular surface. Like trichoid sensilla, they do not project from a specialized basal membrane. There are two distinct forms of s. basiconica in *M. croceipes* described in the present study. The first type, Basiconica A (13.1 \times 2.3 μm), intersperse with more abundant trichoid sensilla on all adult structures examined. Although basiconic sensilla are relatively fewer than trich-



Figs. 3, 4. Midsection of female flagellum. Basiconic sensilla A (BsA); basiconic sensilla B (BsB); campaniform sensilla (CaS); papilla (pp).

oid hairs, they are, nonetheless, as widely distributed. The shaft of Basiconica A is markedly longitudinally grooved or fluted and may project perpendicularly from the cuticular surface. On the flagellum, most hairlike sensory receptors are oriented acropetally (bent toward flagellar tip), thus rendering errant (perpendicular) basiconic hairs more apparent (Fig. 3).

Sensilla Basiconica B (Fig. 4): These blunt-tipped hairs are relatively short ($10.7 \times 2.0 \mu\text{m}$). The shaft is devoid of grooves but has convex protuberances (Fig. 4). Some are acropetally bent about $\frac{1}{3}$ of their length from base of hair.

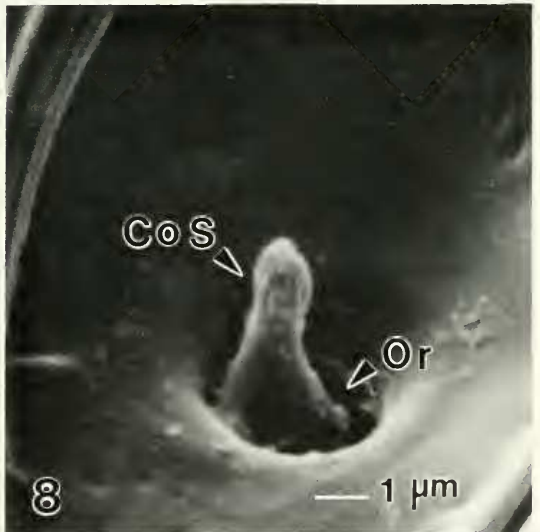
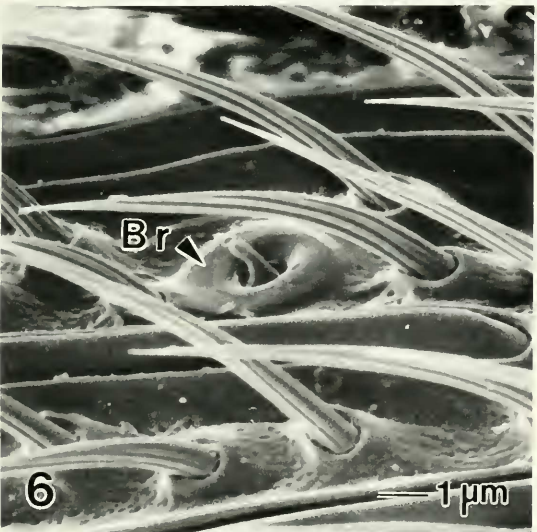
Sensilla Placodea (Figs. 1–3): These elongated sensory plates are found abundantly on all flagellar segments of both sexes. Each plate has a convex inner surface that is slightly elevated above the surface of the flagellum and with a folded ridge surrounding it. The plates on male antennae are ca.

$65.0 \mu\text{m}$ long and $2.8 \mu\text{m}$ wide; on the female, they are ca. $56.6 \mu\text{m}$ long and $3.5 \mu\text{m}$ wide. Male antennal segments are almost twice as long as those of females and have more placoid sensilla organs.

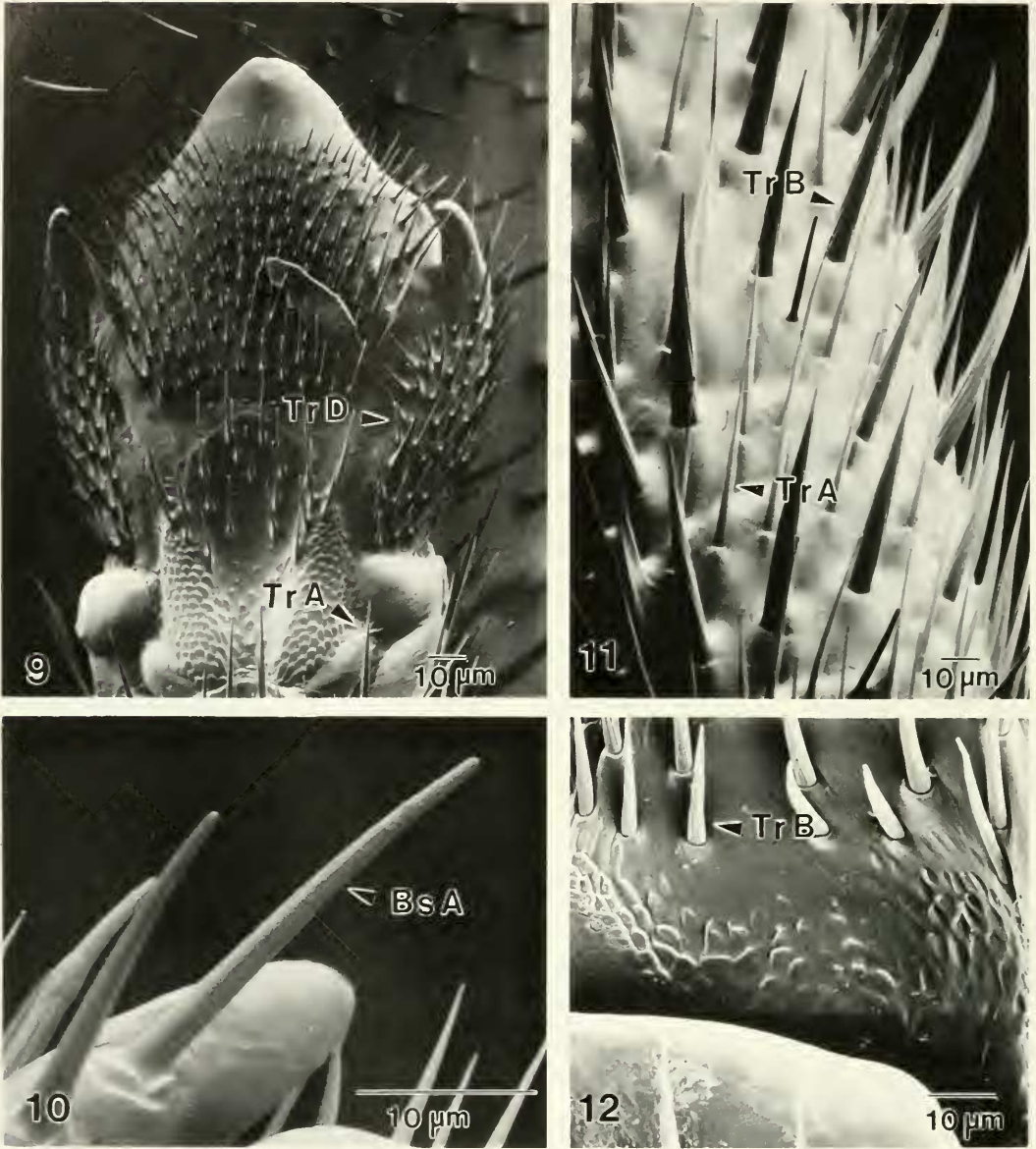
Sensilla Chaetica (Figs. 5, 7): This is the first documentation of the occurrence of these bristlelike sensory receptors in *M. croceipes*. These bristles ($8.1 \times 2.0 \mu\text{m}$) resemble s. trichodea but possess blunt instead of sharply pointed tips typical of trichoid hairs. Each hair articulates on a basal cuticular ring. In *M. croceipes* these sensory bristles were observed on the proximal region of the pedicel normally obscured by a portion of the scape, as well as on the intersegmental membrane between the scape and head. On the latter, these sensilla occur in two distinctly separate groups, one on the dorsal side and the other on the laterodorsal area. The numbers of s. chaetica in each group varied with sex; fewer bristles occurred in females (laterodorsal bristles, 12–17; dorsal bristles, 5) than in males (laterodorsal bristles, 30–31; dorsal bristles, 12). There was no difference in numbers (12) observed on the pedicel of both sexes.

Sensilla Campaniformia (Fig. 4): These platelike sensory structures ($8.3 \mu\text{m}$ dia) are usually circular but sometimes pear-shaped with centrally located papillae ($0.8 \mu\text{m}$ dia). These receptors occur singly only on the distal $\frac{1}{3}$ of flagellomeres 1, 2, 5, 7, 9–11 and 13 of female antennae.

Sensilla Coeloconica (Figs. 6, 8): This type of sensilla was first described in *M. croceipes* as smooth basiconic sensillum (Norton and Vinson 1974b). Scanning electron micrographs revealed that the peglike or conical structure ($2.7 \times 2.6 \mu\text{m}$) projects from an opening (pit) ($3.0 \mu\text{m}$ dia) in the body wall. The peglike projection is also not smooth but rather deeply grooved (Fig. 8) along the distal $\frac{1}{3}$ of its length. Coeloconic sensilla occur singly and dorsocentrally on all flagellar segments of male antennae. The pit is surrounded by a smooth, doughnut-shaped (Fig. 6) cuticular area ($9.0 \mu\text{m}$ dia).



Figs. 5-8. Sensilla chaetica. 5, Portions of scape (upper segment) and pedicel (lower segment) of female antenna. 7, Intersegmental membrane between head and scape. Sensilla chaetica (ChS); trichodea A (TrA); socket (So); dorsal bristles (a); dorsolateral bristles (b). Sensilla coeloconica. 6, Coeloconic sensillum showing the doughnut-shaped basal ring (Br). 8, Coeloconic sensillum showing the orifice (Or) and grooves on distal portion of peg.



Figs. 9-12. Foretarsus. 9 and 10, Close-up view of the pretarsal segment. 11 and 12, Trichoid sensilla B on tarsus.

DISTRIBUTION

On the antennae of *M. croceipes* trichoid, basiconic and placoid sensilla are abundantly present. The scape bears only trichoid sensilla. Sensilla chaetica and s. trichodea (type A) are found on the pedicel. All

sensilla types previously described are found on the antennal flagellum except Trichodea B and D, and s. chaetica.

The foretarsus of *M. croceipes* is divided into pretarsus and 5 tarsal segments. The pretarsus is heavily vested with basiconic (Basiconica A) and trichoid (Trichodea A)

sensilla. Dorsally there are, on average, 136 trichoid sensilla on the arolium pad, 21 on the unguitactor plate and 34 on the lateral plate that extends to the ungues (Fig. 9). A pair of cuticular pads (auxilia) are located basally near the unguitactor plate. The pretarsus bears a distal pore (Fig. 14). The tarsal segments are heavily covered with long, sharply pointed trichoid hairs and sparsely covered with basiconic sensilla. Some trichoids bear spinelike basal projections near the base of the first tarsal segment; the ventral margin is lined with a row of large, round-tipped spines. The maxillary and labial palpi of *M. croceipes* have 5 and 4 segments, respectively (Fig. 17). Compared to the labial palpus, the maxillary palpus is more heavily invested with hairs. Only trichoid (Trichodea A) and basiconic sensilla (Basiconica A and B) were observed on the palpi. Trichoid sensilla occur in larger numbers but basiconic sensilla are larger. The latter are confined mainly to the upper $\frac{2}{3}$ of the segments. The most distal segment of the labial palpus is tipped with a long, robust Basiconica A.

DISCUSSION

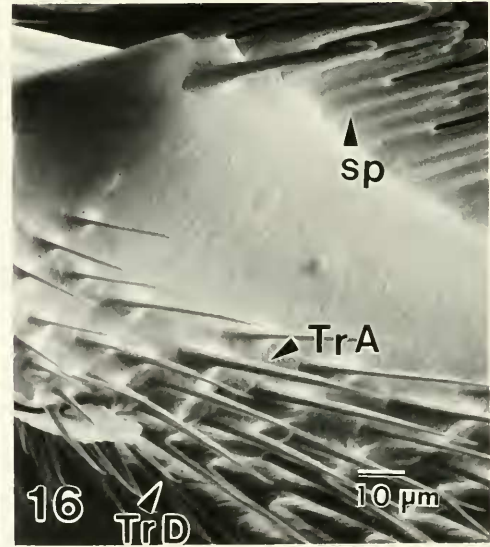
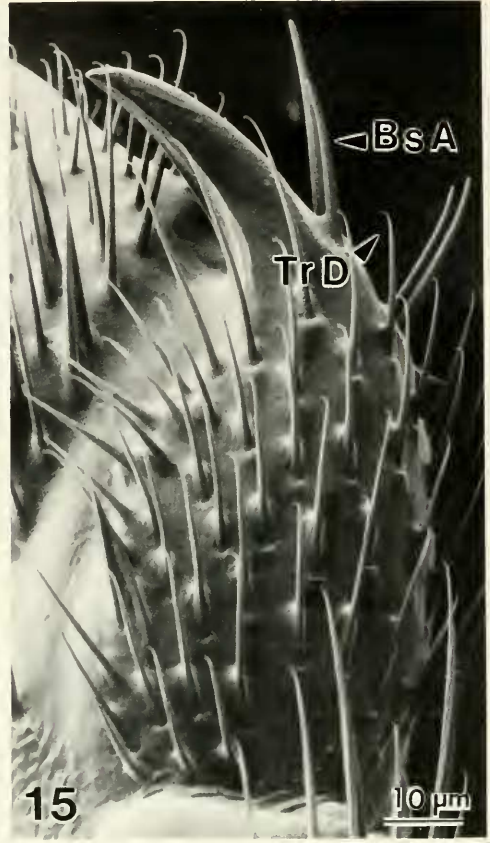
Antennal sensilla have been the subject of several studies in parasitic Hymenoptera because of their active role in host finding (Richerson et al. 1972, Borden et al. 1973, Norton and Vinson 1974a, b, Barlin and Vinson 1981) and courtship behavior (Barrass 1960, Miller 1972). It has long been recognized that insect behavior is often mediated by pheromones received through antennae (Wibel et al. 1984). Weseloh (1972) presented morphological and behavioral evidence showing that in *Chiloneurus noxius* Compere (Encyrtidae) females the organs primarily involved in mediating initial host acceptance behavior are located on the antennae.

The antennae of *M. croceipes*, particularly the flagellar segments, bear the most numerous types of sensilla compared to other structural parts examined. Of the sensilla

types described, trichoid and basiconic sensilla are most ubiquitous.

Trichoid hairs have been reported to perform either or both mechano- and chemosensory functions in pompilids (Alm and Kurczewski 1982, Lane et al. 1988); the presence of an articulating membrane at the base of the hair indicates involvement in mechanoreception. In *Evagetes parvus* (Cresson) the presence of a double chamber in a variant of s. trichodea (Trichodea D) (Lane et al. 1988) suggested their dual function as mechano- and chemosensory receptors. Trichoid hairs on the antennae of *M. croceipes* may be porous or nonporous whereas basiconic hairs are all porous. Porosity of sensory receptors suggests chemosensory function.

Placoid sensilla are common to pteromalids, culophids, braconids, encyrtids, apids, trichogrammatids and aphidiids (Richerson et al. 1972) and occur in predatory pompilids (Alm and Kurczewski 1982, Lane et al. 1988). These sensilla have been implicated in host finding through detection of infrared radiation (Borden et al. 1978, Richerson et al. 1972) and by olfaction (Borden et al. 1978, Schneider 1964). In non-parasitic species placoid sensilla occur on other body parts. For example, in *Urophora affinis* Frauenfeld (Tephritidae), these sensilla located on the ovipositor were involved in chemo- and mechanoreception (Zacharuk et al. 1986). In Hymenoptera placoid sensilla vary in size and shape. They may be elongate and slightly raised above the cuticular surface (e.g. braconids and ichneumonids) (Norton and Vinson 1974b), short and flat (e.g. vespids) (Callahan 1970), or flat and circular (e.g. Apoidea) (Slifer and Sekhon 1960, Dietz and Humphreys 1971, Agren 1977) and may also end in a point (e.g. pompilids) (Walther 1979, Lane et al. 1988). Sensilla chaetica, which articulate individually on a socket, may be involved in mechanoreception. Several classical studies on insect antennae indicate involvement of blunt s. chaetica in mechanoreception. In



Figs. 13-16. 13 and 14, Ventral surface of pretarsus. 15, Dorsal surface of pretarsus. 16, First tarsal segment. Trichoid sensilla A (TrA); trichoid sensilla B (TrB); trichoid sensilla D (TrD); basiconic sensilla A (BsA); distal pore (po); spine (sp).

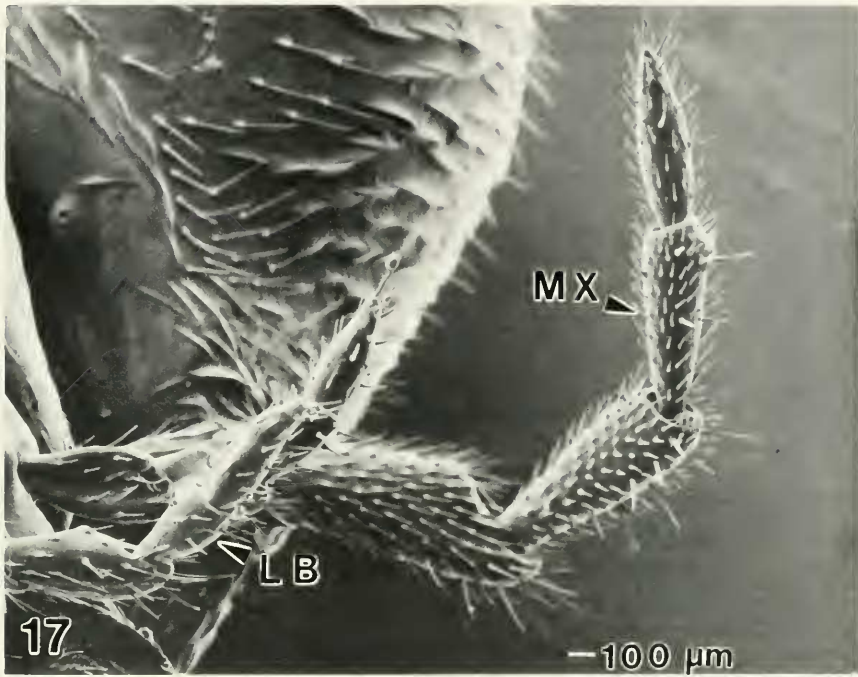


Fig. 17. Maxillary (MX) and labial (LB) palpi beset with trichoid and basiconic sensilla.

honey bee antennae, *s. chaetica* at the two proximal joints were shown to be phasic-tonic mechanoreceptors presumably acting as proprioceptors perceiving antennal position (Schneider 1964). Their specific functions in *M. croceipes*, however, have yet to be determined electrophysiologically.

Like *s. chaetica*, *s. campaniformia* may function as proprioceptors (McIver 1975) and, therefore, generally are considered mechanoreceptors (Dietz and Humphreys 1971). In honey bees, their role in olfaction was negated by earlier studies (Frisch 1921, Dietz and Humphreys 1971).

Sensilla coeloconica have been reported to be involved in CO₂, chemo-, thermo-, and hygroreception (Kuwabara and Takeda 1956, Agren 1977, Altner and Prillinger 1980). In *M. croceipes* these organs occur singly and only on male antennae.

The present study is the first documen-

tation of the occurrence of sensilla Trichodea B, C, and D, basiconic sensilla B, *s. chaetica*, *s. campaniformia* and *s. coeloconica* in *M. croceipes*. Sexual dimorphism, in terms of variation in sensilla types occurring on antennae, is exhibited in *M. croceipes*; bent-tipped trichoid and coeloconic sensilla occurred only on male antennae, and campaniform sensilla were found only on female antennae. Of all the structural parts examined, the antennae bear the most numerous types of sensilla, indicative of their intricate and complex function in modifying adult behavior.

Insect sensilla vary widely in morphology; they occur in a variety of forms, shapes and sizes, and outwardly similar organs may differ considerably in their internal structures. Therefore, information revealed by scanning electron microscopy must be complemented by fine-structural, electrophysi-

ological, behavioral and ablation studies to determine the specific role of each sensillum or receptor type on a particular body part.

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